Torque planning errors affect the perception of object properties and sensorimotor memories during object manipulation in uncertain grasp situations

Abbreviated title: Torque planning errors bias object perception

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1 Abstract

Predicting instead of only reacting to the properties of objects we grasp is crucial to dexterous object manipulation. While we normally plan our grasps according to well-learned associations, we rely on implicit sensorimotor memories when we learn to interact with novel or ambiguous objects. However, little is known about the influence of sensorimotor predictions on subsequent perception and action. Here, young and elderly subjects repeatedly lifted an object in which the center of mass was randomly varied between trials straight upwards with the aim to prevent object tilts. After each lift, subjects indicated the location of the perceived center of mass and reported how heavy the object felt. Surprisingly, we found that sensorimotor torque memories eventually causing initial lifting errors had substantial effects on the perception of torques, weight, and the torque planning for the next lift. Whereas subjects tended to partly retain their previous erroneous sensorimotor memories (instead of solely relying on the previously encountered torque for the upcoming motor plan), they perceived encountered torques stronger when they erroneously predicted them. Additionally, we found that torque prediction errors, as well as the actual torques made the object feel heavier. By contrast, perception did not influence upcoming motor control. There were no major differences observed between the age groups. The sensorimotor impact on torque perception can be explained by internal feedforward prediction highlighting task-relevant errors while the partial retention and adaptation of sensorimotor torque memories is reconciled with the trial-to-trial learning rule for motor adaptation.

2 New & Noteworthy

The current study is the first to demonstrate in an object manipulation task in uncertainty that errors in the sensorimotor prediction of torques influence perception of both torques and weight, whereas sensorimotor torque memories are partly retained and partly adapted to planning errors. Our results

provide novel insights into the predictive mechanisms underpinning the common everyday task of object manipulation and further support theories about the predictive modulation of perception established in other neuroscientific disciplines.

3 Introduction

To grasp and manipulate objects, the incorporation of predicted object properties into a motor plan is crucial to reduce initial motor errors before sensory feedback becomes available and is processed. While a myriad of learned object representations can be accessed through visual cues like size (Gordon et al. 1991), geometry (Fu and Santello 2012), material (Buckingham et al. 2009), object identity (Hermsdörfer et al. 2011) or arbitrary cues (Ameli et al. 2008), action planning relies on object dynamic representations acquired in recent lifts in the absence of informative visual cues. These so called 'sensorimotor memories' are quickly and unconsciously learned to guide force (Johansson and Westling 1984) and torque programming (Lukos et al. 2013) on a trial-to-trial basis.

In addition to shaping the motor plan, internal models are also believed to underpin dynamic forward models by creating predictions of the expected sensory states arising from the execution of the motor plan (Wolpert and Flanagan 2001). By comparing the predicted and the actual sensory input, the CNS monitors the action progress and allows for updating of the internal models. In addition, feedforward predictions of sensory states based on an efference copy of the motor plan have been shown to shape perception by dampening the perception of self-induced action consequence (von Holst 1950). This phenomenon, which presumably exists to highlight externally-caused sensory events, has been demonstrated for eye movements and finger-tip force production (for reviews see: Franklin and Wolpert 2011; Wolpert and Ghahramani 2000).

Studies investigating the interplay of motor prediction and perception in object manipulation yielded surprising findings: In studies in which subjects had to grasp equally heavy objects of different sizes

(Flanagan and Beltzner 2000) or surface material (Buckingham et al. 2009) subjects only initially scaled force rates according to object size or material and quickly harmonized force rates while they persistently judged the lighter-looking object to feel heavier. These findings were interpreted as evidence that these weight illusions were not induced by mismatches of sensorimotor prediction, but rather by violated weight expectations, highlighting the independence of hedonic perception and the control of action. (Flanagan and Beltzner 2000).

Recently however, a pioneering study by (van Polanen and Davare 2015) showed that in the absence of visual cues to object weight, subjects who lifted a light object after having lifted a heavy object over-scaled their force rates and also perceived the lifted object as feeling lighter. This was regarded as the first evidence of an effect of sensorimotor prediction mismatches on weight perception. Furthermore, effects of the mass distribution (Amazeen and Turvey 1996) and the grip force levels (Flanagan and Bandomir 2000; Flanagan et al. 1995) were shown to affect the heaviness perception.

To our knowledge, no previous research has investigated the interplay between errors in torque prediction and perception in a basic object manipulation task. Here, by having subjects lift a neutral object with an unforeseeably varying center of mass, inevitably torque planning errors occur at lift onset. We assess the effect of these on torque and heaviness perception to evaluate whether prediction errors have a task specific or even a generalized effect on perception. We hypothesize that torque planning errors add to torque perception in the direction of the error and furthermore increase the heaviness percepts. Regarding the heaviness perception, we additionally test whether torques per se add to heaviness perception.

Although previous studies of torque prediction in uncertain situations have shown that torques at lift onset partly resemble the previous trial's affordance (Lukos et al. 2013), it is unclear whether sensorimotor predictions are also partly retained. Based on the trial-to-trial learning rule for motor

adaptation (Gonzalez Castro et al. 2014), we predicted that previous sensorimotor predictions still influence performance on upcoming trials, biasing the upcoming torque prediction towards the previous prediction. Furthermore, we explored if conscious perception influences action planning beyond the encountered physical properties, and controlled our findings for unspecific error-reducing delay strategies. To date, no study has yet investigated the age dependency of torque prediction and perception. As groups of young and elderly participants participated in the study, we additionally explored whether these mechanisms are age dependent.

4 Materials and Methods

4.1 Participants

Overall 24 participants, consisting of 12 young (5 female, 7 male, all right-handed, 18-28 years, mean age 22.8 ± 3.4years) and 12 elderly (5 female, 7 male, 10 right-handed, 2 left-handed, 62-76 years, mean age 69.0 ± 4.9 years) individuals with normal or corrected to normal vision took part in the experiment. Handedness was assessed by self-report. All subjects were naïve to the purpose of the study and gave informed consent to participate in the experiment. The experimental procedures were approved by the Institutional Review Board of the Technical University of Munich and were in accordance with the Declaration of Helsinki. All subjects had no history of neurological disorders or musculoskeletal disorders of the involved upper limb and were not under the influence of centrally acting drugs. The participants received a small monetary compensation for their participation in the experiment which lasted ~1.5 hours.

4.2 Experimental Design and Statistical Analyses

4.2.1 Experimental Task and -Procedure and the Experimental Apparatus

Subjects were asked to reach, grasp, lift and replace a custom made, inverted T-shaped grip device originally introduced by (Fu et al. 2010) (see Figure 1 A) consisting of a vertical handle element which was attached over the center of a horizontal bar. The longish grasp surfaces were covered with fine grain sandpaper (Bosch, P320) and allowed subjects to freely choose digit placement. The aluminum panels underneath the grasp surfaces were attached to 6-axis force/torque-sensors (see Data recording below for details) which were concealed from sight. The horizontal bar element contained 5 cavities in which a matching 250 g aluminum weight was randomly positioned prior to each trial. The view of the weight-cavities (and thus the weight distribution of the object) was blocked by a detachable aluminum lid during the trials. A lightweight magnetic position/orientation-tracker (see Data recording below for details) was mounted on top of the horizontal bar. The handle- and bar element each weighed 250 g, resulting in a total object weight of 750 g including the aluminum weight. For each aluminum-weight-position, we calculated the center of mass (CoM) along the horizontal axis in relation to the center line of the grip device and the resulting external torques around a sagittal line through the center with SolidWorks 2014 (Dessault Systems). With negative signs denoting a CoM on the left and accordingly a resulting counter-clockwise external torque, the arising torques amounted to -0.210 Nm, -0.105 Nm, 0 Nm, 0.105 Nm and 0.210 Nm and a respective CoM of -28.4 mm, -14.2 mm, 0 mm, 14.2 mm and 28.4 mm for the weight being placed in the outer left, middle left, center, middle right and outer right cavity (see figure 1B). Subjects used the needle of a digital caliper which was parallel to the horizontal bar and aligned with the right edge of the bar to indicate the perceived center of mass (see figure 1A).

To raise the expectation that total object weight might vary during the course of the experiment, the experimenter initially showed a set of 2 aluminum and 2 plastic weights to the participants and stated that each and any combination of these could be randomly placed in the 5 concealed cavities of the

horizontal bar prior to each trial. Subsequently, all weights were hidden from view throughout the experiment and only one aluminum weight was actually used.

To assure exact alignment with the caliper, the experimenter exactly repositioned the grip device within the marked boundaries on a mousepad at the beginning and after each grasp-to-lift trial before perceptual judgments were made. To guarantee a comfortable limb posture for grasping, we allowed the subjects to initially position and orient the apparatus at their discretion by shifting the underlying mousepad.

The subjects were instructed to reach for the grasp-device with their dominant hand after the first signal tone, grasp it at the grasp surfaces with the fingertips of the thumb-, index- and middle finger and lift it in a natural, not hesitant, movement while preventing the object to tilt to the side. Subjects were aware that they could freely position their fingers on the grasp surfaces while avoiding the edges. Subjects were asked to hold the object at a height of ~10-15 cm until a second tone 4 seconds after the first signaled them to replace the device.

Consequently, subjects should indicate where along the length of the object it could be balanced without tilting (i.e., the center of mass), with the caliper. Then, subjects were asked to give the numerical value that they felt best represented the heaviness of the object they had just lifted. No constraints were placed on this value or its range other than larger numbers representing heavier weights (i.e., absolute magnitude estimation) (Zwislocki and Goodman 1980). After each trial, subjects were asked to close their eyes while the experimenter relocated the aluminum weight (even when the weight position remained the same by chance, the weight was removed and reinserted). Care was taken to ensure that participants could neither visually nor acoustically infer the position of the weight. Overall, each subject lifted the device 100 times and hereby encountered each weight configuration 20 times. The position-sequence was randomly determined for each participant

independently employing the ‘datasample’ function in Matlab 2016a (MATLAB, RRID:SCR_001622) beforehand.

4.2.2 Data Recording

The forces and torques exerted on both sides were recorded by two 6-axis force/torque sensors (ATI Nano-17 SI-50-0.5, ATI Industrial Automation; force range: 50,50, and 70 N for x-, y-, and z-axes, respectively; force resolution: 0.012 N; torque range 0.5 Nm; torque resolution: 0.063 Nmm, sampling rate 200 Hz) and digitally converted and transferred to a laptop by a Net-F/T-Transducer-box (ATI Industrial Automation). A magnetic tracker (TrakSTAR, Ascension Technology Corporation, accuracy: 1.4 mm RMS, 0.5 degrees RMS, sampling rate 200 Hz) was fixed centrally on the top of the horizontal base to digitally record the position and orientation of the device. Data collection was synchronized using custom software written in Matlab 2012 (MATLAB, RRID:SCR_001622).

4.2.3 Data Processing and Task mechanics

Data processing and analysis were conducted with custom software written in Matlab 2016a (MATLAB, RRID:SCR_001622). After data collection, the force/torque data was filtered through a sixth-order Butterworth low-pass filter with a cutoff frequency of 14 Hz.

The crucial time point of lift onset, corresponding to the moment when sensory feedback about object weight and weight distribution becomes available, was defined as the moment 10ms prior to which the vertical position of the object raised above a threshold of 0.2 mm.

We examined the following variables: (1) grip force (GF) was defined as the mean force acting orthogonal against the grasp surfaces, (2) load forces (LFs) were directed upwards on each side of the handle. The center of pressure (CoP) was defined as the vertical distance of the mean center of

159 pressure of the forces applied on each side relative to the sensor reference point and (3) ΔCoP was
160 defined as the difference between the right and the left CoP. Note, that the CoP of the index-and
161 middle finger side relates to a virtual finger combining index and middle finger while the separate
162 positions as well as forces exerted by the two fingers are unknown. (4) The total exerted torque is
163 comprised of two torque components: (a) the torque generated by the product of the side difference
164 between the load forces and half the distance between the grasp-surfaces and (b) the product of the
165 mean grip force and ΔCoP (For details on the task mechanics and the calculation of the CoPs and
166 torques see supplementary Figure S1). To have the exerted torques match in sign with the external
167 torques they compensate for, all clockwise exerted torques were defined as negative and all counter-
168 clockwise torques as positive. The torque exerted at lift onset, prior to sensory feedback about the
169 external torque, is considered a valid indicator of motor torque prediction (Fu et al. 2011; Fu and
170 Santello 2012; Fu et al. 2010; Zhang et al. 2010). The difference between the external torque and the
171 exerted torque is the uncompensated torque corresponding to the net torque acting on the grip device
172 which causes a rotational acceleration after lift onset. We coin the difference between the external
173 torque and the exerted torque at lift onset planning error (5) ($\text{planning error} = \text{external torque} -$
174 $\text{torque at lift onset}$) as indicator of the success of motor torque prediction. As a measure of the task
175 consequence of the planning error before corrections have taken place (Zhang et al. 2010), we
176 measured the peak object tilt in the frontal plane in the first 300ms after lift onset (6). To account for
177 the individual variation in the hesitancy of lift execution, we subject-wise Z-standardized the time
178 from the initial contact of the grasp surfaces until lift onset. The aforementioned variables are
179 illustrated in the representative trial depicted in Figure 2.

180 **4.2.4 Data Management**

181 Due to technical errors 1.5% (35/2400) of the measurements were faulty and the respective
182 observations were discarded. The reported heaviness estimates were subject-wise Fischer z-

183 transformed. The raw caliper values conferred from the digital display were centered to the grip
184 center. It was evident that while some subjects tried to give physically reasonable judgments, others
185 projected their perception of mass asymmetry to the full scale of the caliper ([-106 mm, 106 mm])
186 although the real center of mass varied across a notably closer range ([-28.4 mm, 28.4 mm]) and it is
187 physically impossible to encounter an object which entire mass is concentrated in its edges (see
188 supplementary Figure S7). Therefore, the stated CoMs reflect individual representations of perceived
189 torques to the caliper range, rather than a physical representation of the center of mass. To further
190 focus on this individual representation, we Z-standardized the CoM indications subject-wise. As the
191 object CoM and the resulting torques can be converted and are identical after Z-standardization, we
192 refer to the perceived torque in the following, as torque is the physical quality which can actually be
193 perceived by grasping. The pattern of CoM judgments of participant 4 who alternately declared the
194 CoM to be either on the far left or the far right (see supplementary Figure S7), irrespective of the
195 actual CoM, clearly deviated from all other participants and was deemed unreasonable. As
196 Participant 4 lacked both German and English language fluency, it is possible that this participant did
197 not fully understand the instructions regarding the CoM judgment. Hence, we excluded participant 4
198 from the analysis of perceived torques. Regarding the heaviness perception, some subjects judged the
199 object to be extraordinary light during the first few trials (see supplementary Figure S10). Some
200 subjects reported their surprise about the low weight of the metal surfaced object. As the obvious
201 surprise effect quickly mitigated and distorted the otherwise rather linear time trend, we excluded all
202 heaviness ratings which were 2.5 SD above or below the mean. It was evident that the majority of the
203 subjects considerably varied in their heaviness rating indicating that they perceived weight
204 differences. The statistical models for the exerted torque at lift onset included experimental variables
205 from the previous trial as predictors. As these were missing for the first trial and for each trial
206 following an observation discarded due to technical errors, we had to discard these trials for model

fitting. After data cleaning, the datasets contained 2310 observations for the exerted torque at lift onset-model, 2265 observations (23 subjects) for the perceived torque (Z-score)-model and 2329 observations for the perceived weight (Z-score)-model.

4.2.5 Statistical Analysis

All statistical analyses were conducted in the R environment for statistical computing (version 3.5.0, (R Core Team 2018), R Project for Statistical Computing, RRID:SCR_001905).

Prior to model building, we inspected scatterplots of the response variables against trials and the proposed predictors to judge whether 'trial' should be included as predictor and if the relations between the other predictors and the responses were indeed linear.

To simultaneously test our hypotheses represented by continuous and categorical predictors which hereby control for each other, we chose a multiple linear regression modelling approach. As we were interested in the within person fluctuation of motor prediction and object perception and not person means, we centered raw predictor variables which varied from trial to trial at the individual subject's mean. Hence, these variables represented the within person variation (WP) (Hoffman 2014).

As we conducted 100 trials per subject, the repeated measurements from each individual cannot be assumed to be independent as observations from one person tend to be more similar than observations between subjects, which may lead to a pronounced inflation of the alpha-errors (Aarts et al. 2014). Therefore, we employed linear mixed effects modelling (LMM). In addition to estimating the group effects like classical linear multiple regression models, the so-called fixed effects in LMM, LMM can also estimate how much these predictor effects vary among the randomly selected subjects around the group effects. By including these so-called random effects for predictors whose effect significantly vary among subjects, LMM accounts for the nesting structure of the data

and safeguards against anti-conservative inference (Aarts et al. 2014; Bates et al. 2000; Long 2011). While the fixed effects/ group effects are included according to the research hypotheses and constitute our main research interest, random effects serve to test the significance of the fixed effects appropriately. The appropriate selection of random effects to include in the model is a controversial statistical issue. To keep the model inferences as conservative as possible but without over identifying the model, we adapted a model building approach described by (Bates 2015). In short, starting with the inclusion of all possible random effects, we first iteratively simplified the random effects structures until they were accommodated by the data. Subsequently, we iteratively tested if the remaining random effects significantly contributed to model fit employing Likelihood-ratio-tests between the more complicated candidate model and the simplified candidate model. Random effects not contributing to model fit were eliminated. As seen for the 'perceived torque' model, it is also possible that none of the found group effects significantly vary among participants so that the model can be simplified to a classical multiple linear regression model.

All LMMs were fitted with the restricted maximum likelihood criterion using the ‘lme4’ package (R package: lme4, RRID:SCR_015654, (Bates et al. 2015)). The age groups were dummy coded as 0 and 1, so that interactions of the main effects with the age category represent the difference in the main effect between age groups. We will report the findings for both age groups coded as reference group separately. P values of the fixed effects were obtained by Wald-type t-tests with Satterthwaite’s method for approximating degrees of freedom as implemented in the ‘lmerTest’ package ((R package: lmerTest, RRID:SCR_015656)(Kuznetsova et al. 2016)). We screened for violations of the model assumptions with diagnostic plots assessing the linearity of the predictor effects and model predictions as well as the normality of the residuals and the individual random effects estimates and did not detect worrisome deviations. We further report the standardized β-

252 regression estimates and their respective confidence intervals of significant predictors which were
253 extracted with the 'sjsstats'-package (Lüdecke 2018).

254 The partial effect plots of the significant effects containing 95% prediction intervals derived from
255 parametric bootstrapping of the final models together with conditional partial residuals were
256 computed with the 'visreg'-package (Breheny and Burchett 2017). All plots were created with the
257 'ggplot2' package (Wickham 2016) (ggplot2, RRID:SCR_014601) and the modifications introduced
258 in the 'cowplot' package (Wilke 2017). As an overall measure of goodness of fit, we report pseudo-
259 R^2 statistics for the fixed effects and random effects of LMMs computed with the 'piecewiseSEM'
260 package (Lefcheck 2016) which follows the procedure described in (Nakagawa and Schielzeth 2013)
261 and the R^2 statistic for the classical multiple linear model. Pseudo-R^2 values, analogous to the R^2
262 measure in classic multiple linear regression, approximate how much of the overall response variance
263 is explained by the model.

264 **4.2.5.1 Modelling the Exerted Torque at Lift Onset**

265 The exerted torque at lift onset was regarded a valid proxy of the sensorimotor memories guiding
266 torque planning, as feedback about the actual external torque is only available after lift onset. We fit
267 two complementary models whose sets of predictors allow us to test different hypotheses. As the
268 external torque equals the sum of the exerted torque at lift onset and the torque planning error (i.e. the
269 difference between the external torque and the exerted torque at lift onset), two of the three above-
270 mentioned predictors must be included in a regression model and the meanings and interpretations of
271 each depends on the other. Regarding overall model prediction, both models lead to virtually equal
272 predictions. In the first model, we included the previous external torque and previous torque planning
273 error. Hence, the coefficient of the previous external torque indicates the degree to which current
274 torque prediction reflects the object properties at the last trial, while the coefficient of the previous

planning errors is informative about the role of previous sensorimotor memories relative to the actual previous torque on upcoming torque prediction. The planning error can be envisaged as vector pointing from the exerted torque at lift onset towards the external torque (see Figure 2). While a positive correlation coefficient of the previous planning error would indicate a shift of the torque at lift onset towards the previous external torque, a negative sign would indicate a shift at lift onset towards the previous erroneous torque at lift onset. A coefficient which did not differ from zero would provide no evidence against the assumptions that the CNS fully discards previous sensorimotor memories in favor of a plan which only incorporates previous object dynamics. However, a negative coefficient would indicate that the torque prediction is shifted towards the previous sensorimotor plan, reducing the alignment of the motor plan with the previous task dynamic, while a positive sign would suggest that the previous erroneous plans are not only discarded but even reversed, hence leading to a better alignment with the previous task dynamic than if no error was made. The first model allows us to compare our findings with previous object manipulation studies (e.g. (Lukos et al. 2013)).

In force-field-perturbation studies, the trial-to-trial learning rule for motor adaptation (reviewed in (Gonzalez Castro et al. 2014; Ingram et al. 2011)) is a conventional motor learning model which assumes that the states of a sensorimotor memory of object dynamics are partly retained and partly adapted according to the experienced prediction error: $x(n+1) = \propto * x(n) + \beta * e(n),$ where x(n) is the state of the model on trial n, α is the retention coefficient, β is the adaptation-rate, and e is the error given by the difference between the perturbing force and the model state. Hence, by including the previously exerted torque at lift onset as a proxy of the previous state of sensorimotor memory, and the previous planning error as a proxy for the sensed prediction error, the respective coefficient of the previously exerted torque at lift onset is informative about sensorimotor retention while the regression coefficient of the previous planning error is informative about the degree to which an

adaptation of the previous sensorimotor model towards previous task dynamics has occurred, with a positive sign denoting adaptation towards the previous external torque.

This analysis allows us to compare our findings with studies employing inconsistently changing force-fields (Gonzalez Castro et al. 2014).

Both models also included the 'perceived torque (Z-score) at the previous trial', to test for an effect of conscious perception on action, the 'external torque at the current trial', to control for unspecific corrections, as well as the 'age group' and the 'contact to lift onset time (Z-score)' as fixed main effects. Furthermore, the models contained the interactions of the aforementioned predictors with the age category as well as the all possible two- and three-way interactions among the 'external torque at the current trial', the 'contact to lift onset time (Z-score)' and the 'age group'. The exploratory plots suggest no trial effect (see supplementary Figure S2) and rendered the assumption of a linear relation between the predictors and the response as reasonable (see Figure S3). The necessary random effects were separately determined such that the final first LMM contained the random variances of the Intercept, the current external torque, the 'planning error at the previous trial', the 'external torque at the previous trial' and the 'perceived torque (Z-score) at the previous trial', while for the second LMM the 'Intercept', and the slopes of the 'torque at lift onset at the previous trial WP', the 'planning error at the previous trial WP', the current external torque and the 'contact to lift onset time (Z-score)' were considered as necessary independent random effects.

4.2.5.2 Modelling the Perceived Torque (Z-score)

The exploratory plots suggest no trial effect (see supplementary Figure S8) and rendered the assumption of a linear relation between the predictors and the response as reasonable (see Figure S9). During the mixed effects model building process all tested random effects were deemed unnecessary as they did not improve model fit. Therefore, the final model was a classical multiple linear

regression model with the 'perceived torque (Z-score)' as dependent variable and the 'external torque' and 'planning error WP at the current trial' as well as their interaction as the predictors chosen for confirmatory hypothesis testing. Additionally, the main effect of the 'age group' and the interactions between the other predictors and the 'age group' were included.

4.2.5.3 Modelling the Perceived Weight (Z-score)

The scatterplot of the weight percepts across trials (see supplementary Figure S10) suggests a linear trial trend after the exclusion of outliers. The non-parametric 'loess'-regression curves overlaid over the scatterplots of the weight percepts across the external torque and the planning error (see Figure S11) resemble parabolas. Therefore, we included the trial-number, the linear terms of the external torque and the planning error WP and age group as well as the quadratic terms of the external torque and planning error WP as fixed main effects. Like before, the model further contained the main effect of age group and all fixed interaction effects with age group. Our final model included the subject specific independent random effects of the linear and quadratic effect of the external torque and the linear term of the planning error as well as the covariance between the random effects of the aforementioned linear terms.

5 Results

5.1 Predictive Torque Control: Exerted Torque at Lift Onset

In the present study the peak object tilt was highly correlated with the planning error at lift onset (Pearson's $R^2 = 0.84$) demonstrating the behavioral importance of the planning error measure.

In the first model the negative Intercept (young: -0.012 [Nm], t(22.0)= -2.709, p= 0.013); elderly: -0.018 [Nm/Nm], t(22.0)= -4.054 [Nm], p= 0.000528) suggests that subjects tend to exert a small clockwise torque at lift onset when the external torques and the torque perception are centered and no

prediction error had occurred. The exerted torque at lift onset is positively correlated with the external torque encountered at the previous trial (which is uncorrelated with the external torque at the current trial due to random sampling) (young 0.4139 [Nm/Nm], β=1.019, t(53.7)=15.331, $p< 2*10^{-16}$, elderly 0.3915 [Nm/Nm], β=0.964, t(30.7)= 16.857, $p< 2*10^{-16}$, see Figure 3A) as well as negatively correlated with the planning error at the previous trial (young -0.2134 [Nm/Nm], β=-0.508, t(58.2)= -6.131, $p= 8.21*10^{-8}$, elderly -0.1306 [Nm/Nm], β=-0.311, t(34.37)= -4.283, p=0.000141, see Figure 3 B). Noteworthy is the opposite direction of these effects: While planned torques partly reflect the previously experienced external torque, occurring planning errors lead to a shift of the subsequent torque prediction to the direction of the erroneous previous prediction. Thus, the participants seemed to partly adhere to previous mispredictions instead of fully discarding previous sensorimotor prediction or even inversing them in the direction of the previous error. Although the effect of the planning error is highly significant in both age groups, the slopes appear to differ (see Figure 3 B)). However, this interaction between 'planning error WP' and 'age group' did not reach statistical significance (p=0.08). We further detected a smaller, yet highly significant, correlation with the external torque of the current trial (see Figure 3 C and Figure 4 C) which was included in the models to control for motor corrections taking place before lift onset was registered. Given our very low height threshold of only 0.2 mm used for lift onset detection and the subtraction of 10 ms from the time point at which the threshold was reached, any motor corrections before the determined moment of lift onset were assumed to depend on a self-imposed object-lift delay after the gravitational force was, at least at one object side, matched. Therefore, we hypothesized that a potential effect of the external torque of the current trial might interact with the time between contact and lift onset. Hence, we included the Z-standardized 'contact to lift onset time' and its interactions with 'external torque' and 'age group' to control for the effect of Z-standardized hesitancy. Therefore, the main effect of 'external torque' (young: 0.096 [Nm/Nm], β=0.236, t(22.6)= 7.984, $p= 5.07*10^{-8}$; elderly: 0.131

[Nm/Nm], β= 0.321, t(22.2)= 10.883, p= $2.31*10^{-10}$) represents the effect for lifts conducted with the individual average speed. The effect increases with the individual standardized contact to lift onset time (young: 0.0335 [Nm/SD], β=0.081, t(2248)= 4.089, p= $4.48*10^{-5}$; elderly: 0.0305 [Nm/SD], β= 0.074, t(2165)= 3.991, p= $6.79*10^{-5}$), while the interaction of the main effect with the age group just failed to achieve significance (p=0.055). Elderly subjects also seemed to generate a marginally more clockwise torque with increasing time to lift onset (main effect of 'contact to lift onset (Z-score)' elderly: -0.0034 [Nm/SD], β= -0.056, t(22.23)= -2.174, p= 0.041). These results indicate that participants hesitated to lift the object after counteracting the gravitational force and added a small delay used for minor motor corrections in which the object was held at an undetectably low hovering state. Thus, although the measure 'torque at lift onset' is majorly determined by predictive processes, the motor strategy of hesitancy around the lift onset biases the measure towards the current external torque such that the real planning error is slightly underestimated.

Although the exploratory raw scatterplot (see Figure S3 D) which included a simple linear regression line hints at a linear relationship between the 'perceived torque' and torque planning, we found no such effect in our final model (p=0.52). By controlling for the effects of the previous external torque (see also figure S5) and previous planning error which are highly correlated with the torque perception (see section 5.2), this lack of a detectable relationship implies that the conscious torque percept does not include any additional cognitive information salient to the sensorimotor system beyond the aforementioned influential variables.

In the second model the predictor 'torque at lift onset at the previous trial' was employed instead of the 'external torque at the previous trial'. Hence, the main effect of the previously exerted torque at lift onset (young: 0.418 [Nm/Nm], β= 0.404, t(32.0)= 14.66, p= $9.27*10^{-16}$; elderly: 0.391 [Nm/Nm], β= 0.378, t(19.4)= 15.883, p= $1.47*10^{-12}$) represents the positive retention rate of previous

sensorimotor memories (see figure 4 A) and the main effect of the previous torque planning error WP (young: 0.199 [Nm/SD], β= 0.472, t(57.3)= 5.917, p= $1.93*10^{-7}$; elderly: 0.2507 [Nm/SD], β= 0.596, t(32.6)= 8.596, p= $6.84*10^{-10}$, see figure 4 B) the adaptation rate of feedback-errors in parallel to the trial-to-trial learning rule for motor adaptation (e.g. (Gonzalez Castro et al. 2014)). None of the remaining predictors not found significant in the first model reached significance, while the significant effects of the Intercept (young: -0.013 [Nm], t(22.0)= -2.8, p= 0.010); elderly: -0.018 [Nm/Nm], t(22.0)= -4.057 [Nm], p= 0.000525), the current external torque (young: 0.096 [Nm/Nm], β= 0.237, t(22.6)= 8.007, p= $4.83*10^{-8}$; elderly: 0.130 [Nm/Nm], β= 0.318, t(22.1)= 10.837, p= $2.61*10^{-10}$, see Figure 4 C) and the interaction between the current external torque and the contact-to lift onset time (Z-score) (young: 0.0340 [Nm/SD], β=0.082, t(2254)= 4.142, p= $3.58*10^{-5}$; elderly: 0.0310 [Nm/SD], β= 0.075, t(2164)= 4.045, p= $5.41*10^{-5}$) as well as the negligible main effect of contact to lift onset (Z-score) in the elderly (-0.0034 [Nm/SD], β= -0.056, t(22.19)= -2.149, p= 0.043) were virtual identical to the estimates of the first model.

The Pseudo-R^2 of the fixed effects explains about 49.4% (I)/ 49.6% (II) of the overall variance and the random effects add an additional 12.2% (I)/ 11.5% (II) of variance explained.

The change in the sign of the regression coefficient of the 'previous planning error WP' between the two models is determined by the complimentary predictors 'previous external torque' in the first model and 'previous torque at lift onset WP' in the second model (as can be visually inferred from Figures S4 and S6). This stands in line with the deviating interpretations of the coefficients of the planning-error in the two models.

5.2 Torque Perception (Z-score)

Subjects perceived the torques according to the actual torque (young: 2.365 [SD/Nm], β= 0.354, t(2259)=10.244, $p< 2*10^{-16}$; elderly: 2.743 [SD/Nm], β= 0.410, t(2259)=13.916, $p< 2*10^{-16}$) and additionally to the committed planning error WP (young: 4.107 [SD/Nm], β = 0.592, t(2259)= 17.179, $p< 2*10^{-16}$; elderly: 3.449 [SD/Nm], β= 0.497, t(2259)= 16.765, $p< 2*10^{-16}$). The interaction between these two main effects (p=0.517) as well as the 3-way interaction with age group (p=0.406) were insignificant suggesting that the effects are independent from each other. The effect of the external torque was similar for both age groups ('external torque x age group' interaction: p= 0.21), while the effect of the planning error on torque perception was smaller in the elderly group (-0.658 [SD/Nm], β= -0.065, t (2259) = -2.086, p= 0.037). Remarkably, the untransformed estimates [Nm/Nm] as well as the standardized β coefficients [SD/SD] and the partial effect plots (see Figure 5) seem to convey that the committed planning errors had a stronger impact on the torque perception than the physical size of the encountered external torque, at least in the young group, while the influences rather seemed of similar strength in the elderly group.

The adjusted coefficient of model determination R^2 indicates that 82.9% of the total variance was explained by the model.

5.3 Heaviness Perception (Z-score)

On the first lift when no torque nor planning error was present (= Intercept), participants judged the object to feel significantly lighter than on their individual average (young: -0.807 [SD], t(2282)= -14.003, $p< 2*10^{-16}$; elderly: -0.763 [SD], t(2268)= -12.899, $p< 2*10^{-16}$). Heaviness percepts linearly increased in the course of trials (young: 0.008 [SD/trial], β=0.234, t(2245)= 8.873, $p< 2*10^{-16}$; elderly: 0.008 [SD/trial], β=0.234, t(2257)= 8.844, $p< 2*10^{-16}$). There was a quadratic relationship between both the external torque (main effect of External $Torque^2$: young: 13.20[SD/Nm^2], β=0.267, t(2256)= 6.233, $p= 1.87*10^{-9}$; elderly: 11.991 [SD/Nm^2], β=0.243, t(1577)= 6.405, $p= 1.65*10^{-9}$) and

the planning error WP (main effect of Planning Error^2: young: 7.532 [SD/Nm^2], β=0.165, t(2299)= 3.988, p= 6.86*10^{-5}; elderly: 7.266 [SD/Nm^2], β=0.159, t(2273)= 4.722, p= 2.48*10^{-6}), while the linear terms of these predictors were insignificant. This indicated that the minimum point of the parabola is horizontally centered at zero. None of the interactions with age reached significance. Figure 6 depicts the results.

The Pseudo-R^2 of the fixed effect is 19.4% with the random effects increasing the Pseudo-R^2 by 4.0%. This points towards a moderate overall model fit at most.

6 Discussion

The study aimed to examine the role of sensorimotor torque planning errors on the subsequent perception of object characteristics, and whether previous torque planning error, in addition to the previously encountered torque, impacted the upcoming torque planning.

6.1 Predictive Torque Control

A previous study on predictive torque exertion in uncertainty (Lukos et al. 2013) did not investigate whether previous sensorimotor model states were discarded or partly retained or even inversed according to error in the next trial in addition to updating the model state according to the encountered external torque. We hypothesized that sensorimotor memories in uncertain grasp situations do not completely decay to be overridden by last trials external torque from trial to trial, but are also partly retained. We modelled the torque prediction in two complementary ways. By selecting the previous external torque and the previous planning error as predictors in the first model, we confirmed a strong role of the previous external torque on the current torque while we could also show that subjects partly adhere to their erroneous predictions. As the externally acting torques in our experiment resemble force-field-perturbations and the exerted torques at lift onset and the planning

error can be regarded as proxies of the states of the sensorimotor memory and the feedbacked error respectively, our second model corresponds to the parameters of the trial-to-trial learning rule for motor adaptation established in force-field studies (for review see (Gonzalez Castro et al. 2014)). In accordance with that model, we found that sensorimotor memories were partly retained and partly adapted towards the occurring planning error. Whereas it takes only a few trials to learn predictive torque- (Zhang et al. 2010) or grip force- (Johansson and Westling 1988) control in real object manipulation, it takes up to 30 trials to adapt to novel force fields (Gonzalez Castro et al. 2014). In both, object torque prediction (Lukos et al. 2013) as well as force-field perturbations (Gonzalez Castro et al. 2014) the learning rates were slower when unforeseeable and repeated alterations occurred. Here, the unstandardized adaptation rates were smaller than the retention rates, while the standardized rates were of similar size. Hence, the formation of sensorimotor memories in uncertainty cannot be regarded as one-trial-learning process but as partial trial-to-trial adaptation of previous sensorimotor predictions towards experienced planning errors. As a consequence, the influence of prior trials on the current motor plan might reach further than the last trial. However, as the learning of torques normally occurs in a few trials, we expect sensorimotor carry-over- or after-effects to quickly mitigate after a few trials. Our finding that conscious sensory torque percepts did not contribute to upcoming sensorimotor torque prediction is consistent with previous studies which have shown that even explicit visual percepts of the mass distribution of an object cannot be utilized for torque prediction (Craje et al. 2013; Salimi et al. 2003).

6.2 Torque Perception

This study is the first to demonstrate that torque perception is strongly influenced in the direction of a planning error, defined as the not compensated external torque, which corresponds to the arising net torque. The regression model estimates even suggest that the effect of the planning error may be comparable or, at least in young participants, even stronger than the effect of actual external torque.

As we did not find evidence for an interaction between the planning error and the external torque, we assume that these factors additively account for the perception of torques. Therefore, both a sensory suppression of the veridical torque percept as well as sensory highlighting of the sensorimotor error might underlie this perceptual bias.

To infer the veridical external torque, the CNS must estimate the applied compensatory torque during the phase in which the object is held straight and steady after possible corrections. Therefore, the CNS must integrate available sensory feedback indicating the torque. Central feed forward models of action-and object dynamics are assumed to be utilized to predict the sensory consequences of planned actions on the basis of a reafference copy of the motor plan (Franklin and Wolpert 2011). By persistently comparing the predicted and sensed bodily states, the CNS simultaneously enhances the acuity of end point estimation in reach movements (Adamovich et al. 1998; Bhanpuri et al. 2013) while using forward model predictions to attenuate predicted sensory feedback caused by self-generated movements (von Holst 1950). Concerning the factors relevant for our task, (Shergill et al. 2003) demonstrated that self-generated fingertip pressure was perceived weaker than externally applied pressure of the same magnitude. While the perception of the CoP displacement was found to be exaggerated when load forces diverge (Shibata et al. 2014), the active grasp-to-lift movements did not alter the CoP-displacement perception compared to the perception of passively displaced CoPs (Shibata et al. 2014). Hence, a possible predictive attenuation of self-generated forces resulting in torques might lead to a reduced emphasis on the perception during the highly foreseeable, stable lift phase in which the veridical torque can be inferred best. However, as (Craje et al. 2013) reported that individuals who repeatedly lifted an object with a stable asymmetrical weight distribution judged the CoM accurately, the extent of sensory attenuation in our experiment remains unclear.

When a torque planning error is made, however, this leads to a visual, proprioceptive and tactile percept of the arising rotational acceleration and object tilt which, as it was unexpected, might be attributed as having an external cause. As the initial object tilt, which is highly correlated with the planning error, is often associated with the danger of fluid spillage or loss of object control in daily life, it could be assumed that the error is particularly salient for the perceptive systems. In summary, the percept of the veridical torque during a stable object hold might be inferred by a predominantly tactile afference of well-predictable self-exerted forces, whereas the unforeseen signal arising from erroneous torque planning are probably perceived by visual, proprioceptive, and tactile inputs and experienced as externally caused. Therefore, the percept of the external torque could be exposed to predictive sensory attenuation while the planning error seem to be a sensible candidate for perceptual highlighting.

6.3 Weight Perception

Here, we sought to determine whether sensorimotor planning errors not related to weight prediction per se can also cause a weight illusion, while controlling for the influences of torques on weight perception.

Interestingly, we found that both the actual external torque as well as the planning error were quadratically related to an increase in heaviness perception. The effect of the external torque on heaviness perception stands in line with studies in which participant perceived wielded objects with more eccentric mass distributions as heavier (Amazeen and Turvey 1996). Sensorimotor errors in the adaptation of peak grip force rates prior to lift onset were recently shown to be correlated with the heaviness perception of a light object, when a heavier object was lifted before (van Polanen and Davare 2015). Here, we provide novel evidence that also not-weight related high-level sensorimotor error signals can induce misperceptions of object weight. It is worth noting that the current results, as

well as the finding of (van Polanen and Davare 2015), do not contradict the findings related to fingertip force adaptation in weight illusion studies found, where participants alternately lift objects of equal weight but differing size (Flanagan and Beltzner 2000) or material (Buckingham et al. 2009). In these studies participants were found to quickly adjust their force planning to the equal weight while continuing to judge the less heavy-looking objects to be heavier. However, while proving that the found weight illusions were not caused by sensorimotor error, the studies were not suited to examine the effect of sensorimotor errors on weight perception in a general sense as they quickly mitigated after only a few lifts.

Taken together, our findings support the theory presented by (van Polanen and Davare 2015) that both long term expectations as well as implicit, quickly learnt sensorimotor memories, shape both motor planning as well as perception. While the study designs of (Buckingham et al. 2009; Flanagan and Beltzner 2000) emphasize the impact of priors, the changes in object properties in our study and (van Polanen and Davare 2015) highlight the impact of sensorimotor prediction on weight perception. Overall the experience of object weight seems to extend beyond the veridical sensory judgment of the physical size of weight and integrates effects of violations of expectations, erroneous force prediction as well as not heaviness related object properties and planning errors

6.4 Conclusion

In summary, we provided evidence that the CNS employs feedforward predictive models to refine both upcoming motor predictions and shape the percept of object properties. While the motor system partly retained previous sensorimotor memory states and partly adapted them towards experienced errors instead of solely relying on sensory feedback, the perceptual system emphasized sensorimotor feedback leading to a perception biased in the direction of previous errors. While sensorimotor predictions impact the perception of both task-specific and unspecific object properties, no

549 contribution of conscious percepts on sensorimotor planning were detected. All major findings were
550 highly significant for both young and elderly participants.

551 6.5 Limitations

552 In daily object manipulation torques usually arise when objects are grasped at an eccentric handle or
553 surface, e.g. when grasping a cup or a plate. Therefore, geometric visual cues in addition to
554 sensorimotor memories guide predictive torque control and possibly also influence our object
555 perception when dealing with familiar objects. However, although less frequent, we are confronted
556 with unknown objects which conceal their mass properties, e.g. parcels. We also interact with objects
557 without looking carefully forcing us to rely more on implicit sensorimotor memories (Hesse et al.
558 2016), similar to the experimental situation in the present study. Nevertheless, the interplay of visual
559 cues, sensorimotor mechanisms and perception underlying the control of torques in daily life remains
560 to be investigated in future studies.

561 7 Conflict of Interest

562 The authors declare no competing financial interests.

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10 Figures

Figure 1: Experimental setup. The custom-built grip-device consists of a handle element mounted centrally on a horizontal bar (A, B). The handle element allowed subjects to freely choose digit placement on the sandpaper (Bosch, P320) covered gasp surfaces (40 x 120mm) (A). The aluminum panels underneath the surfaces were mounted on 6-axis-force/torque sensors and blocked the sensors from view (The panels are rendered transparent for illustrative purposes in B). A magnetic position/ orientation tracker was mounted centrally on the horizontal bar (A). A 250g aluminum weight was randomly placed into the 5 cavities of the horizontal bar. The hereby resulting horizontal positions of the center of mass and the external torques arising after lift onset in the vertical object orientation are denoted in B. The orange circle denotes the center of mass of the grip device with the aluminum weight placed in the right cavity (B). A detachable lid blocked the cavities from view (A). To indicate their perception of the center of mass/ the external torque, subjects used the needle of a digital caliper which was parallel to the horizontal bar and aligned with the right edge of the grip device (A).

Figure 2: Representative trial illustrating the task variables. The upwards directed load force sum (LF) exceeds the gravitational force prior to object lift onset (thick vertical line). The mean grip force (GF) acting orthogonal towards the grasp surfaces causes friction preventing finger slip. In order to prevent object tilt, the total exerted torque must compensate for the external torque (horizontal dashed line in the torques subplot) which is depicted for the moment of lift onset with a perfectly vertical object orientation. For the calculation of the exerted torque see supplementary Figure S1. The planning error denotes the difference between the external torque and the exerted torque at lift onset, hence the uncompensated- or net torque at lift onset and is envisaged as vector pointing from the exerted torque at lift onset towards the external torque. The planning error is highly correlated with the peak object tilt occurring in the first 300 ms after lift onset (thin dashed vertical line).

682 Figure 3: Partial effects plots of the significant main effects of the first linear mixed effects
683 regression model for the exerted torque at lift onset with 95% prediction intervals of the effects
684 computed by parametric bootstrapping and partial residuals. The effects are separately plotted for
685 both age groups. As the external torque has discrete values, we display the distribution of the data
686 with box and whiskers plots in the style of Tukey. The central horizontal line represents the median,
687 while the lower and upper hinges correspond to the 25th and 75th percentiles, respectively. The
688 upper and lower whiskers extend from the upper and lower hinge to the largest value no further
689 than 1.5 * inter-quartile ranges from the respective hinges. Data beyond are plotted individually.
690 Additionally, the means are indicated by a ‘X’.

691 Figure 4: Partial effects plots of the significant main effects of the second linear mixed effects
692 regression model for the exerted torque at lift onset with 95% prediction intervals of the effects
693 computed by parametric bootstrapping and the partial residuals. The effects are separately plotted for
694 both age groups. As the external torque has discrete values, we display the distribution of the data
695 with box and whiskers plots in the style of Tukey with additional ‘X’ denoting the means.

696 Figure 5: Partial effects plots of the significant main effects of the multiple linear regression model
697 for the perceived torque with 95% prediction intervals and the partial residuals. The effects are
698 separately plotted for both age groups. As the external torque has discrete values, we display the
699 distribution of the data with box and whiskers plots in the style of Tukey with additional ‘X’
700 denoting the means.

701 Figure 6: Partial effects plots of the significant main effects of the linear mixed effects regression
702 model for the perceived weight with 95% prediction intervals of the effects computed by parametric
703 bootstrapping and the partial residuals. The effects are separately plotted for both age groups. As the

external torque has discrete values, we display the distribution of the data with box and whiskers plots in the style of Tukey with additional ‘X’ denoting the means.

11 Supplementary Material

Figure S1: Task mechanics. Panel A illustrates the forces 'F' exerted on the object in a 3-finger tripod grip, with the left hand with the subscript 'ind' denoting the index finger, 'mi' the middle finger and 'th' the thumb. The registered torques around the z-axis of the F/T-Sensors T_{z_i} result from the sum of the product of the load force F_{y_i} of the respective side and the distance between the grasp surface and the sensor surface a (a=2.4 mm) and the product of the grip force of the respective side F_{x_i} and the vertical CoP_i relative to the sensor reference point: $T_{z_i} = a * F_{y_i} + CoP_i * F_{x_i}$. Therefore, the center of pressure (CoP) relative to the sensor reference point in the center of each sensor surface can be calculated as: $CoP_i = \frac{T_{z_i} - a * F_{y_i}}{F_{x_i}}$. Panel B depicts the external and exerted torques acting on the object around an axis which goes through the center between the F/T-sensors parallel to the z-axis and the variables necessary for calculation. The external torque $T_{external}$ arising at lift onset is caused by the mass asymmetry of the object and is equivalent to the product of the gravitational force vector of the device $F_{G_{total}}$ and the horizontal center of mass CoM_h: $T_{external} = F_{G_{total}} * CoM_h$. As a convention, we denote clockwise external torques and compensating counter clockwise exerted torques as positive. The exerted torque is comprised of two components: (1) the product of the side difference between the load forces ΔLF ($\Delta LF = F_{y_{right}} - F_{y_{left}}$) and half the distance between the grasp-surfaces w/2 (w/2 = 20 mm): $T_{tangential} = \frac{w}{2} * \Delta LF$; (2) the product of the grip forces of each side which can be approximated as equal $F_{x_1} \approx F_{x_2} \approx GF_{mean}$ and the difference of the vertical positions of the CoPs between the grasp sides ΔCoP ($\Delta CoP = CoP_{right} - CoP_{left}$): $T_{CoP*GF} = \Delta CoP * GF_{mean}$. Hence, the total exerted torque equals: $T_{exerted} = \frac{w}{2} * \Delta F_y + \Delta CoP * GF_{mean}$.

Figure S2: Exerted torques at lift onset plotted against trial per age group with overlaid group-wise 'loess'- regression lines and density lines of the distributions. Evidently, the torque at lift onset was

scaled to a similar degree across trials and age groups. The exerted torques at lift onset fluctuated around a marginally clockwise average torque, presumably due to the majorly right handedness of the subjects. Horizontal dashed lines indicate the maximal external torques which had to be compensated for (± 0.21 Nm).

Figure S3: Scatterplots of the exerted torque at lift onset plotted against A) the external torque at the previous trial, B) the planning error WP at the previous trial, C) the external torque at the current trial, D) the perceived torque (Z-score) at the previous trial and E) the exerted torque at lift onset at the previous trial. Distinct plots for both age groups are presented. As the external torque has discrete values, we display the distribution of the data with box and whiskers plots in the style of Tukey. The central horizontal line represents the median, while the lower and upper hinges correspond to the 25th and 75th percentiles, respectively. The upper and lower whiskers extend from the upper and lower hinge to the largest value no further than 1.5 * inter-quartile ranges from the respective hinges. Data beyond are plotted individually. Additionally, the means are indicated by a 'X'.. The subplots contain simple linear regression lines for illustrative purposes which do not correspond to the inferential multiple regression model results and the partial effect plots depicted in Figure 3 and 4.

Figure S4: Scatterplots of the exerted torque at lift onset plotted against the previous planning error WP, plotted separately by the previous external torque and the age group. The subplots contain simple linear regression lines for illustrative purposes. For each previous external torque, the torque at lift onset is negatively correlated with the previous planning error.

Figure S5: Scatterplots of the exerted torque at lift onset plotted against the previous perceived torque (Z-score), plotted separately by the previous external torque and the age group. The subplots contain simple linear regression lines for illustrative purposes. Controlling for the previous external

torque, there seems to be no obvious correlation of the torque at lift onset with the previous torque percept (Z-score).

Figure S6: Three-dimensional Scatterplots of the Torque at lift onset plotted against A) the previous planning error and the previous external torque and B) the previous planning error and the previous exerted torque at lift onset. The scatterplots contain linear regression surfaces based on the regression with the two respective predictors for illustrative purposes. The values of the torque at lift onset are color coded. While A) depicts a negative correlation between the torque at lift onset with the previous planning error while controlling for the previous external torque, the correlation is positive in B) when controlling for the effect of the previous exerted torque at lift onset instead.

Figure S7: Indicated and actual center of mass (CoM) plotted across trials for each participant. The inner-dashed lines represent the actual range of the CoM, the outer-dashed lines the full caliper range which fully spans the object's base. Evidently, participants considerably differed in the range of their estimates. Participant 4 seemed to alternately indicate positions on the left and the right, irrespective of the actual CoM and was therefore removed from further analysis.

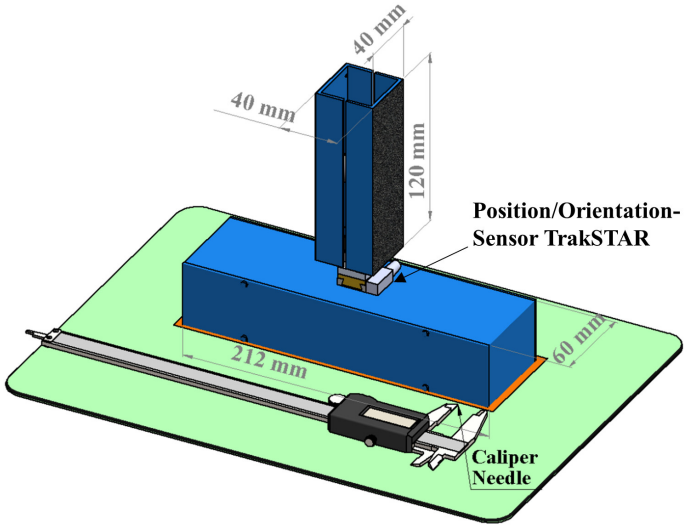
Figure S8: Perceived torques at lift onset plotted against trial per age group with overlaid 'loess'-regression lines and density lines of the distributions. The perceived torques evenly fluctuate around zero. Interestingly the distribution of the torque percepts seems to be trimodal in both age groups.

Figure S9: Scatterplots of the perceived torque (Z-score) plotted against the planning error WP, plotted separately by the external torque and the age group. The subplots contain simple linear regression lines for illustrative purposes which do not correspond to the inferential multiple regression model results and the partial effect plots depicted in Figure 5.

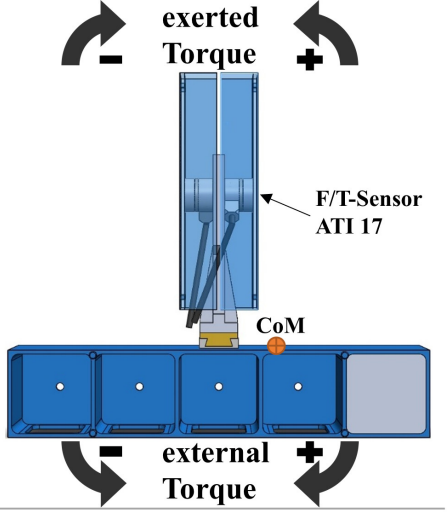
Figure S10: Weight ratings (Z-scores) plotted against trial per age group with overlaid 'loess'-regression lines and density lines of the distributions. Several subjects perceived the heaviness as outlying low during the very first trials. After the first trials the percepts seem to evenly fluctuate across trials with the non-parametric regression line suggesting a linear increase across trials. The distribution of the percepts is comparable in both age groups. Horizontal dashed lines indicate ± 2.5, ± 2 and ± 1 SDs.

Figure S11: Scatterplots of the perceived weight (Z-score) plotted against A) the external torque and B) the planning error WP. As the external torque has discrete values, we display the distribution of the data with box and whiskers plots in the style of Tukey with additional 'X' denoting the means The subplots plots contain non-parametric 'loess'-regression lines for illustrative purposes which do not correspond to the inferential multiple regression model results and the partial effect plots depicted in Figure 6.

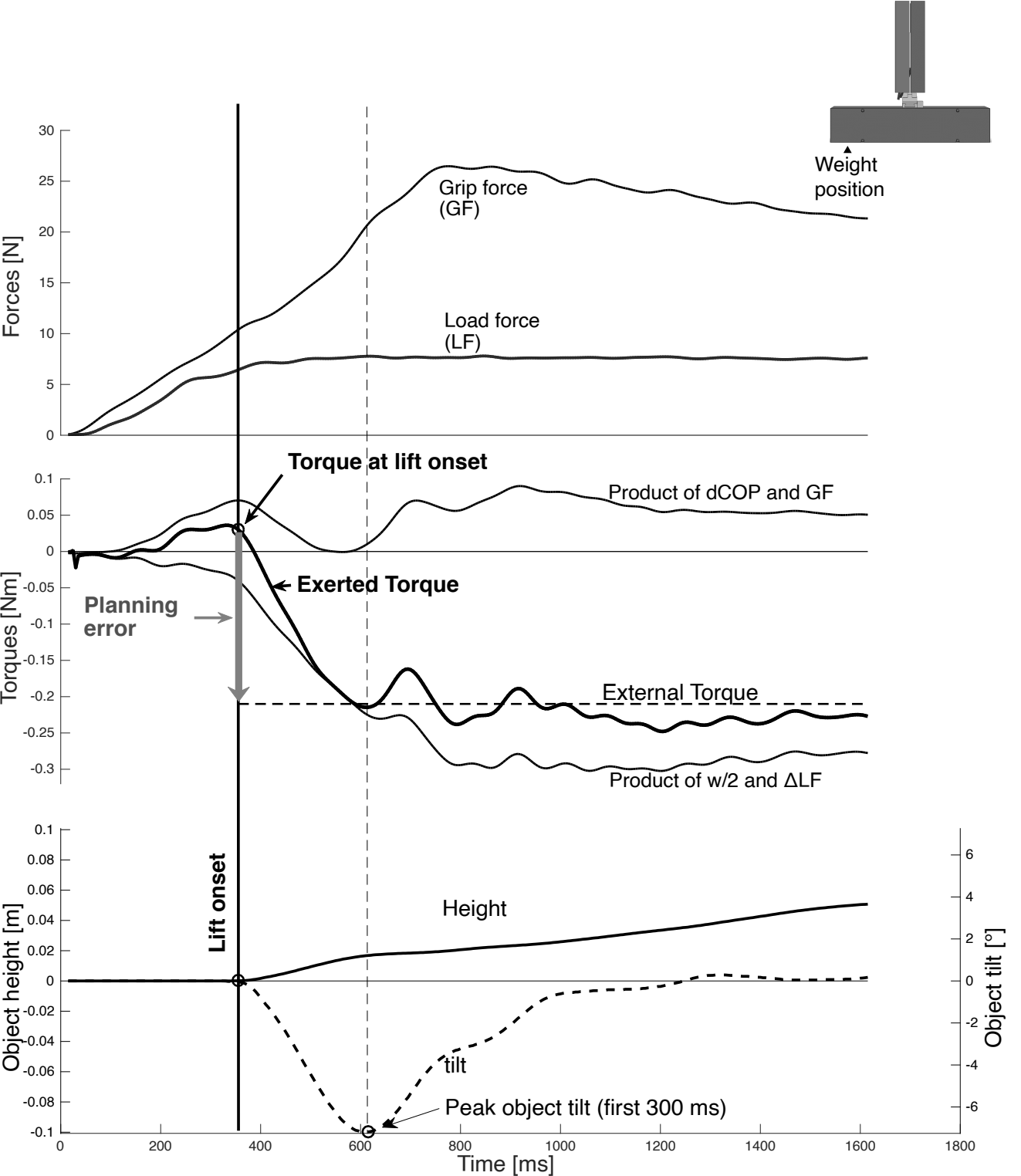
A

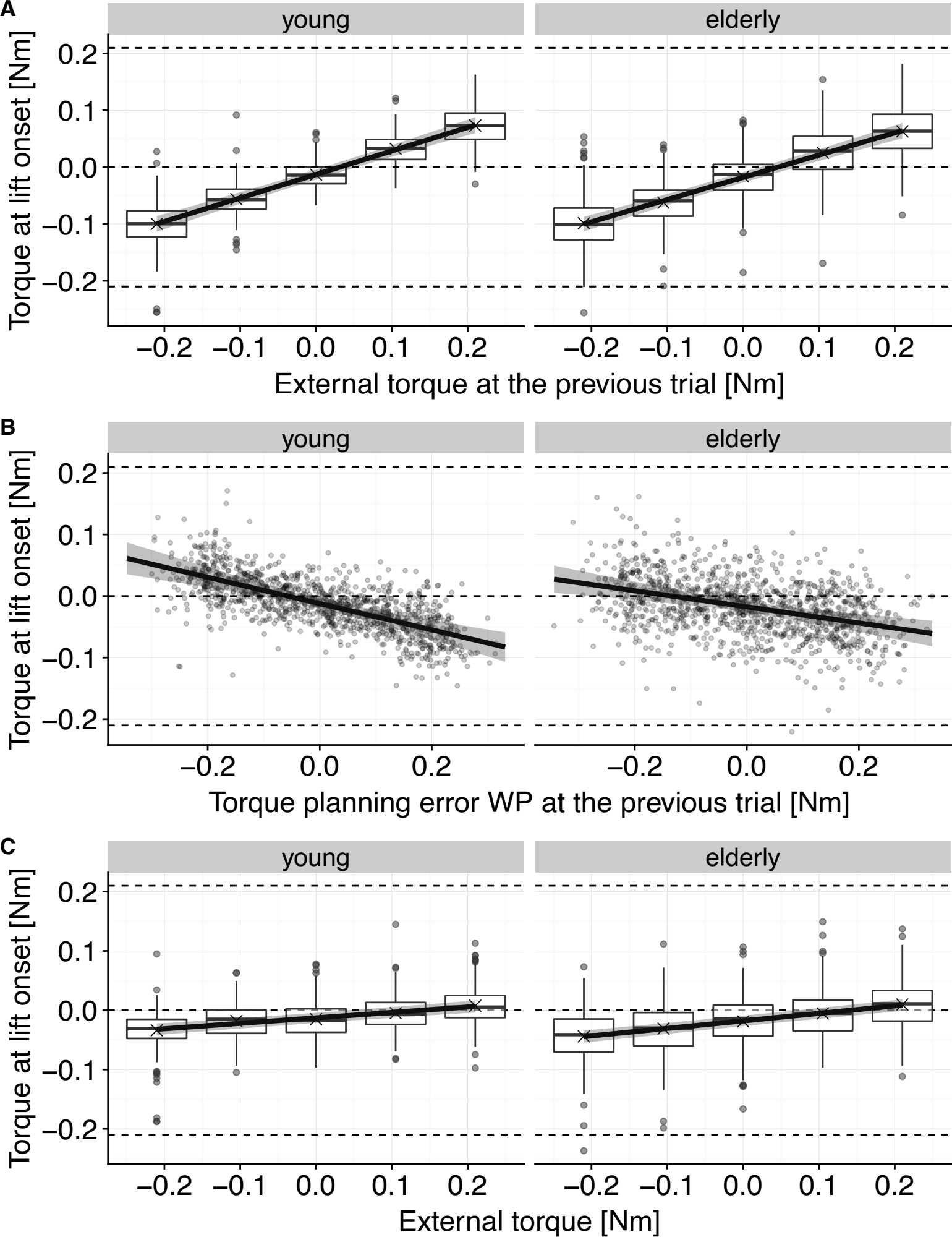


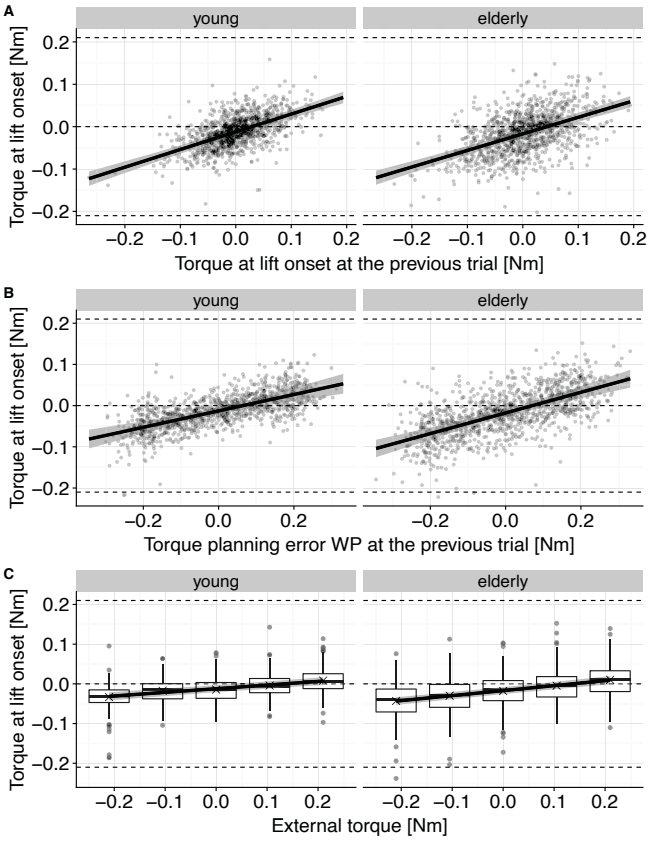
B

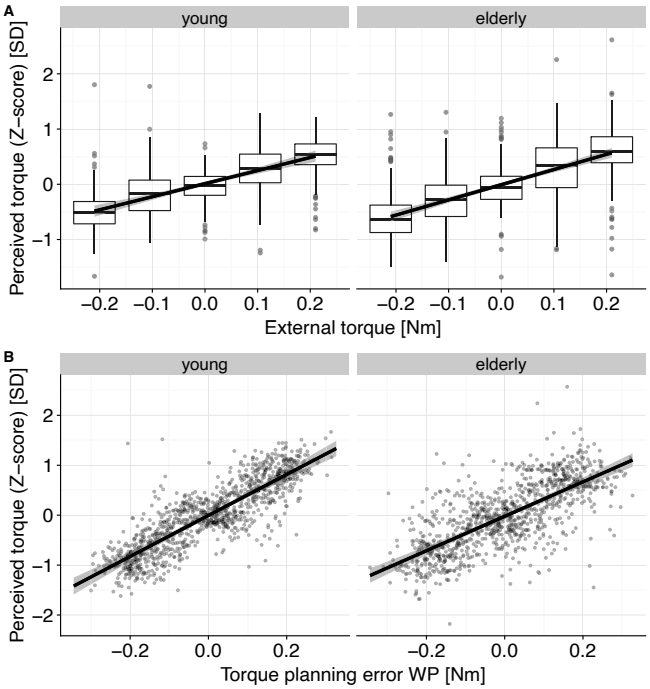


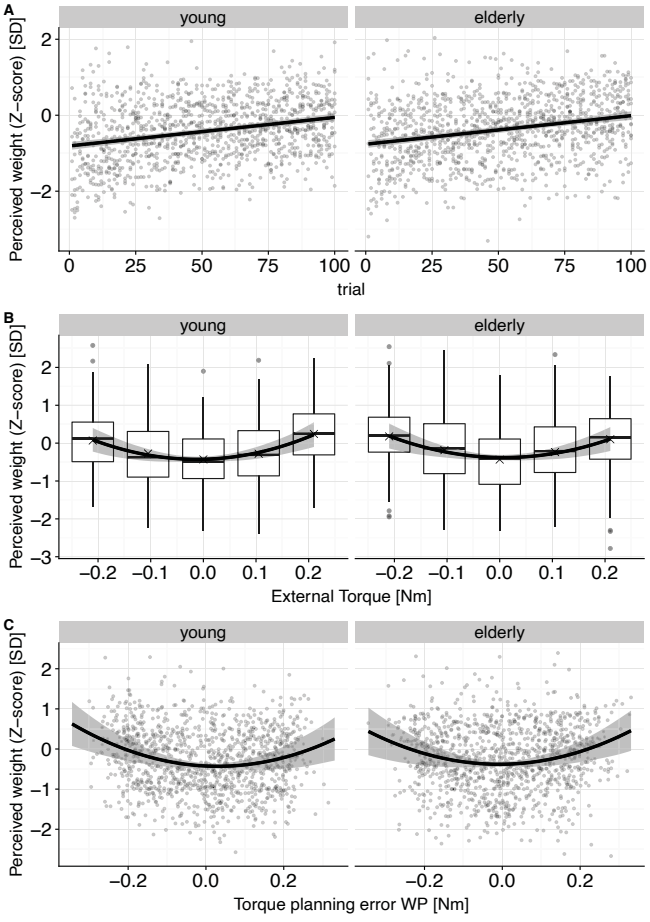
External Torque [Nm]	**-0.21**	**-0.105**	**0**	**0.105**	**0.21**
Center of mass [mm]	**-28.4**	**-14.2**	**0**	**14.2**	**28.4**

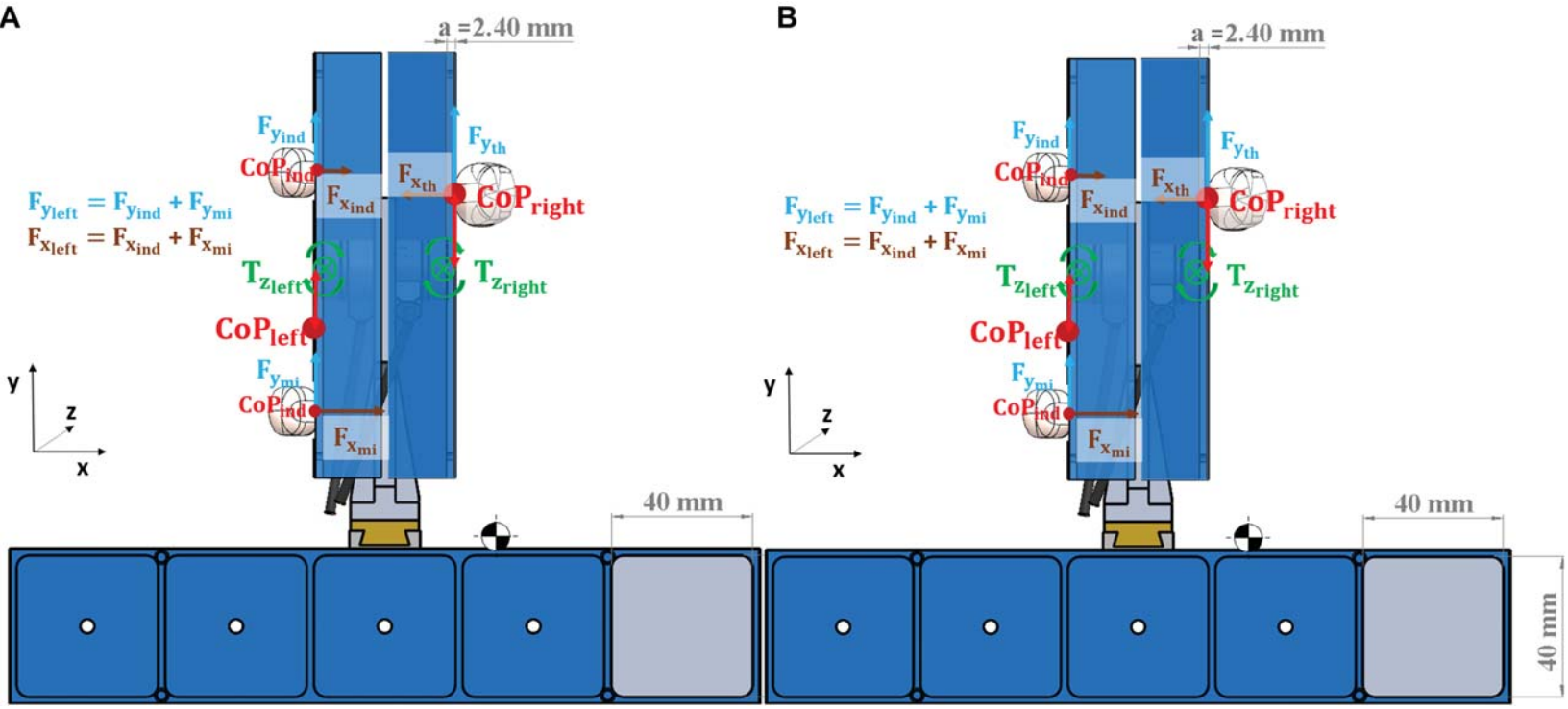

Weight position
Grip force (GF)
Load force (LF)
Forces [N]
Torque at lift onset
Product of dCOP and GF
Exerted Torque
Planning error
External Torque
Product of w/2 and ΔLF
Torques [Nm]
Lift onset
Height
tilt
Peak object tilt (first 300 ms)
Object height [m]
Object tilt [°]
Time [ms]

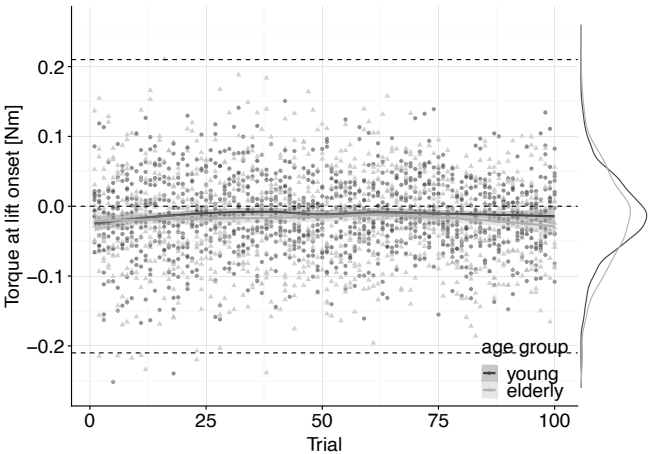

A
young
elderly
Torque at lift onset [Nm]
0.2
0.1
0.0
−0.1
−0.2
−0.2
−0.1
0.0
0.1
0.2
External torque at the previous trial [Nm]
B
young
elderly
Torque at lift onset [Nm]
0.2
0.1
0.0
−0.1
−0.2
−0.2
0.0
0.2
Torque planning error WP at the previous trial [Nm]
C
young
elderly
Torque at lift onset [Nm]
0.2
0.1
0.0
−0.1
−0.2
−0.2
−0.1
0.0
0.1
0.2
External torque [Nm]

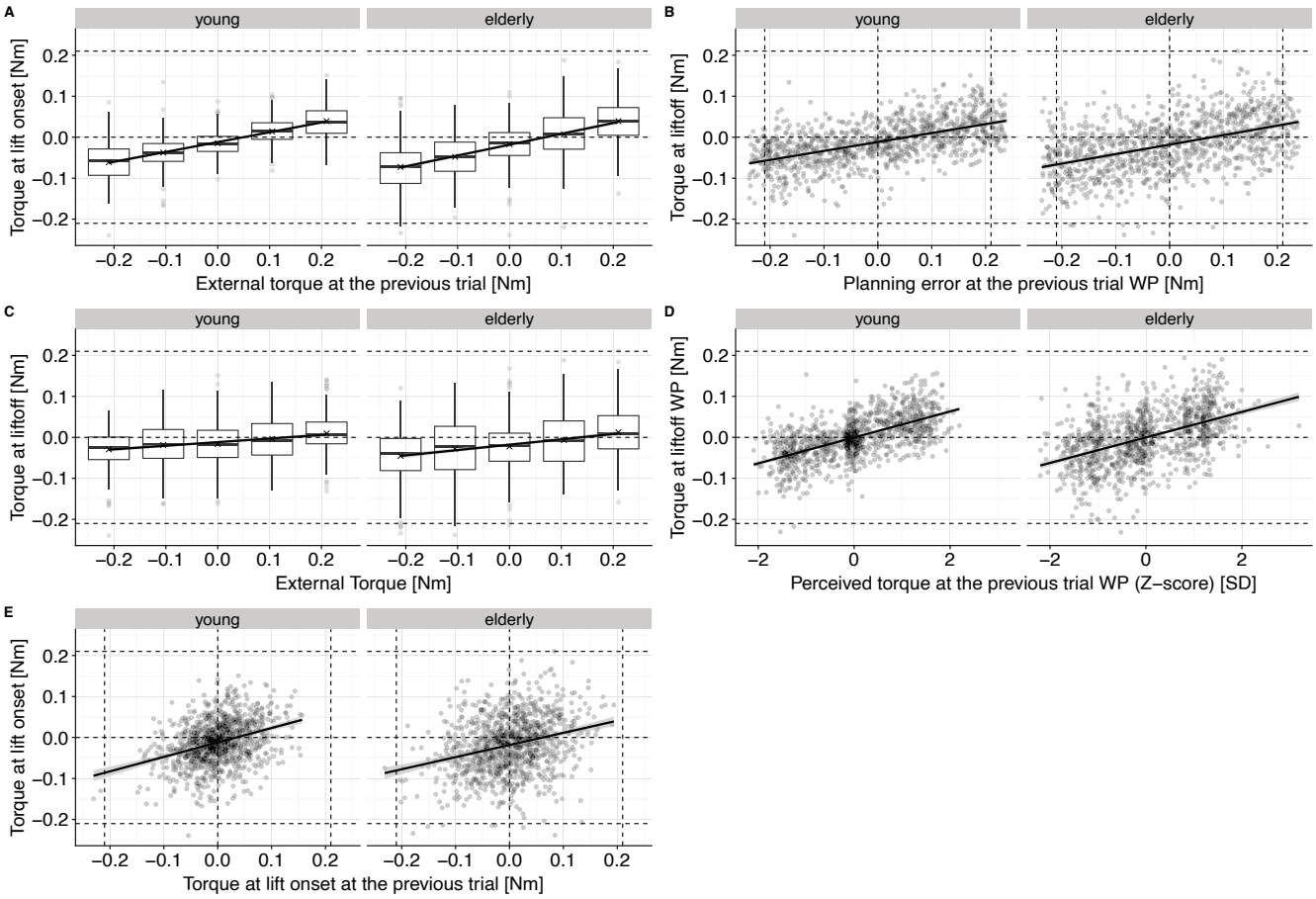

A
young
elderly
Torque at lift onset [Nm]
0.2
0.1
0.0
−0.1
−0.2
−0.2 −0.1 0.0 0.1 0.2
Torque at lift onset at the previous trial [Nm]
B
young
elderly
Torque at lift onset [Nm]
0.2
0.1
0.0
−0.1
−0.2
−0.2 0.0 0.2
Torque planning error WP at the previous trial [Nm]
C
young
elderly
Torque at lift onset [Nm]
0.2
0.1
0.0
−0.1
−0.2
−0.2 −0.1 0.0 0.1 0.2
External torque [Nm]

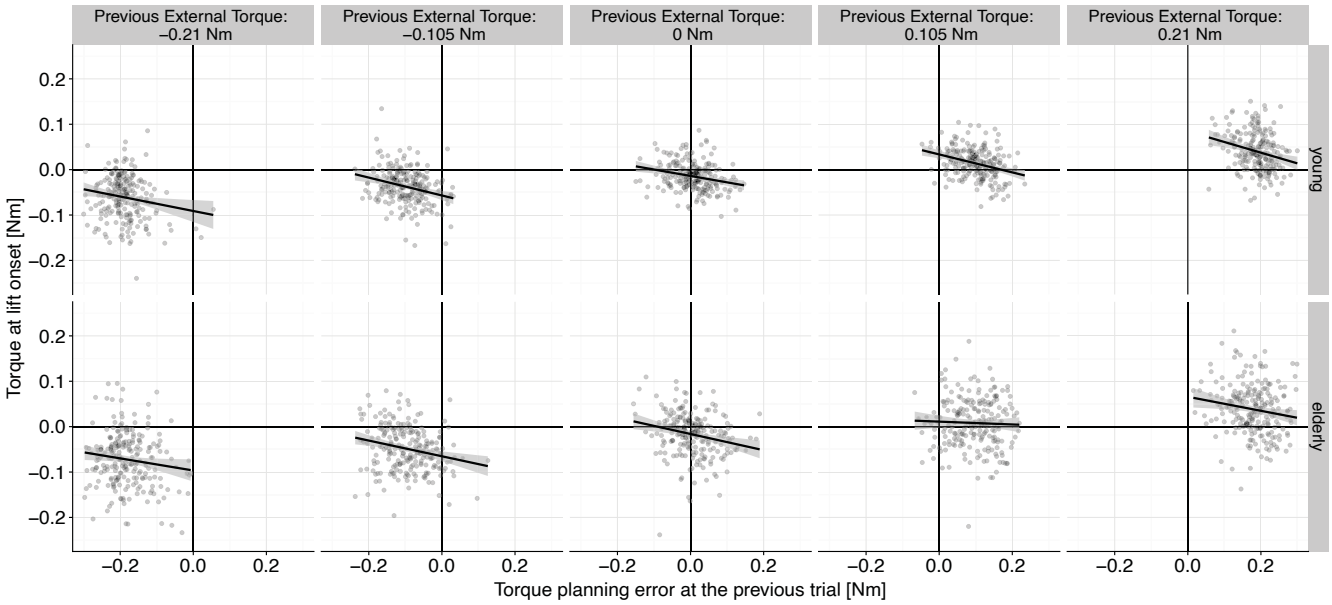

A
young
elderly
Perceived torque (Z−score) [SD]
2
1
0
−1
−0.2
−0.1
0.0
0.1
0.2
External torque [Nm]
B
young
elderly
Perceived torque (Z−score) [SD]
2
1
0
−1
−2
−0.2
0.0
0.2
Torque planning error WP [Nm]

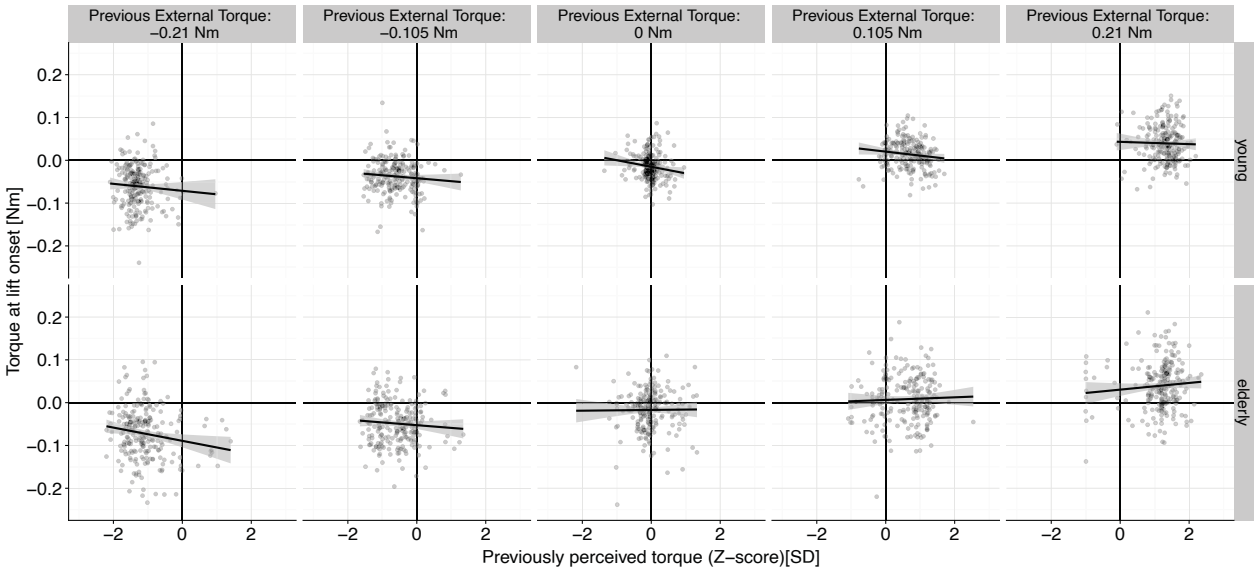

A
young
elderly
Perceived weight (Z−score) [SD]
2
0
−2
0
25
50
75
100
trial
B
young
elderly
Perceived weight (Z−score) [SD]
2
1
0
−1
−2
−3
−0.2
−0.1
0.0
0.1
0.2
External Torque [Nm]
C
young
elderly
Perceived weight (Z−score) [SD]
2
1
0
−1
−2
−0.2
0.0
0.2
Torque planning error WP [Nm]

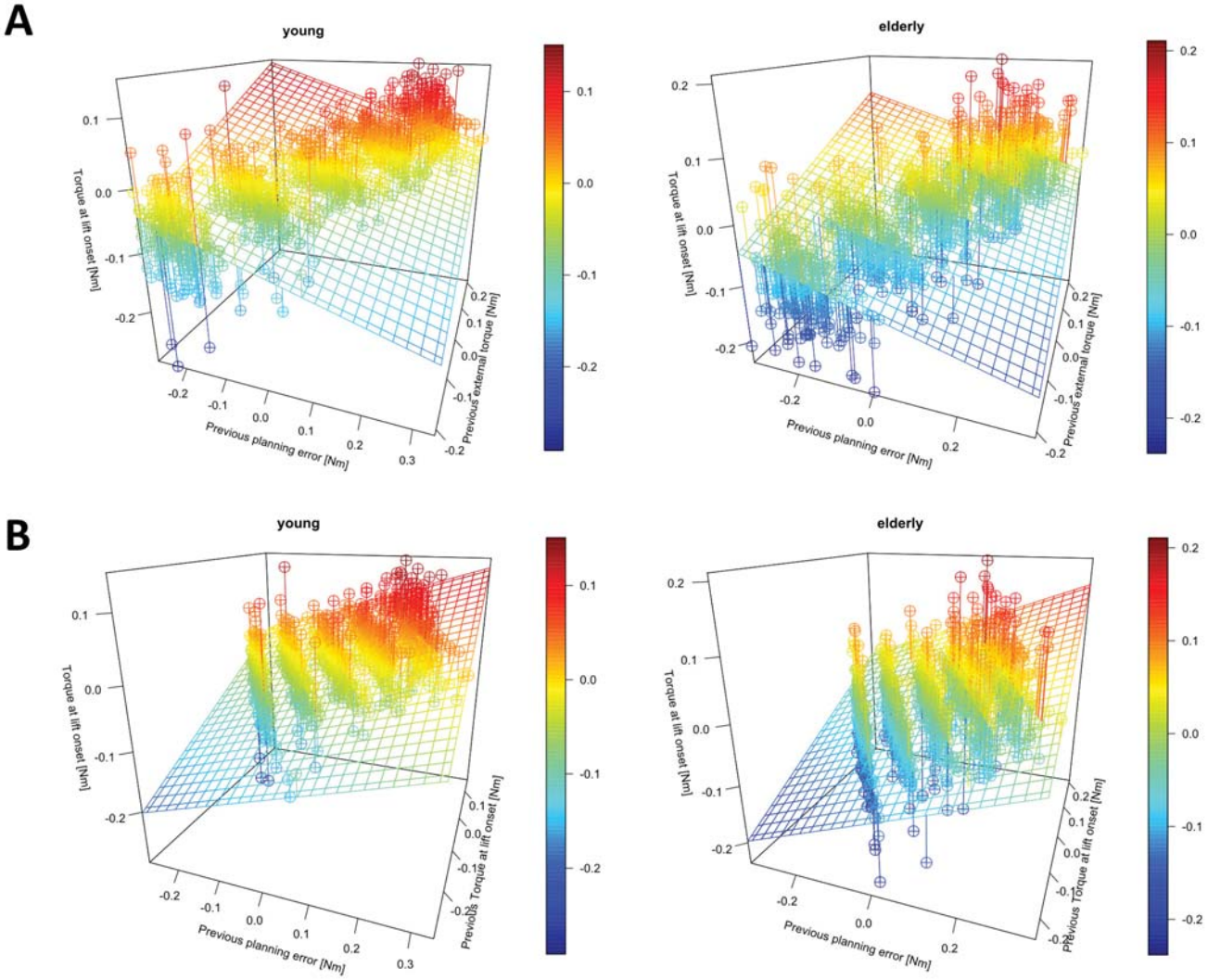

A
a =2.40 mm
$F_{y_{left}} = F_{y_{ind}} + F_{y_{mi}}$
$F_{x_{left}} = F_{x_{ind}} + F_{x_{mi}}$
$F_{y_{ind}}$
CoP_{ind}
$F_{x_{ind}}$
$F_{y_{th}}$
$F_{x_{th}}$
CoP_{right}
$T_{z_{left}}$
$T_{z_{right}}$
CoP_{left}
$F_{y_{mi}}$
CoP_{ind}
$F_{x_{mi}}$
y
z
x
40 mm
B
a =2.40 mm
$F_{y_{left}} = F_{y_{ind}} + F_{y_{mi}}$
$F_{x_{left}} = F_{x_{ind}} + F_{x_{mi}}$
$F_{y_{ind}}$
CoP_{ind}
$F_{x_{ind}}$
$F_{y_{th}}$
$F_{x_{th}}$
CoP_{right}
$T_{z_{left}}$
$T_{z_{right}}$
CoP_{left}
$F_{y_{mi}}$
CoP_{ind}
$F_{x_{mi}}$
y
z
x
40 mm
40 mm

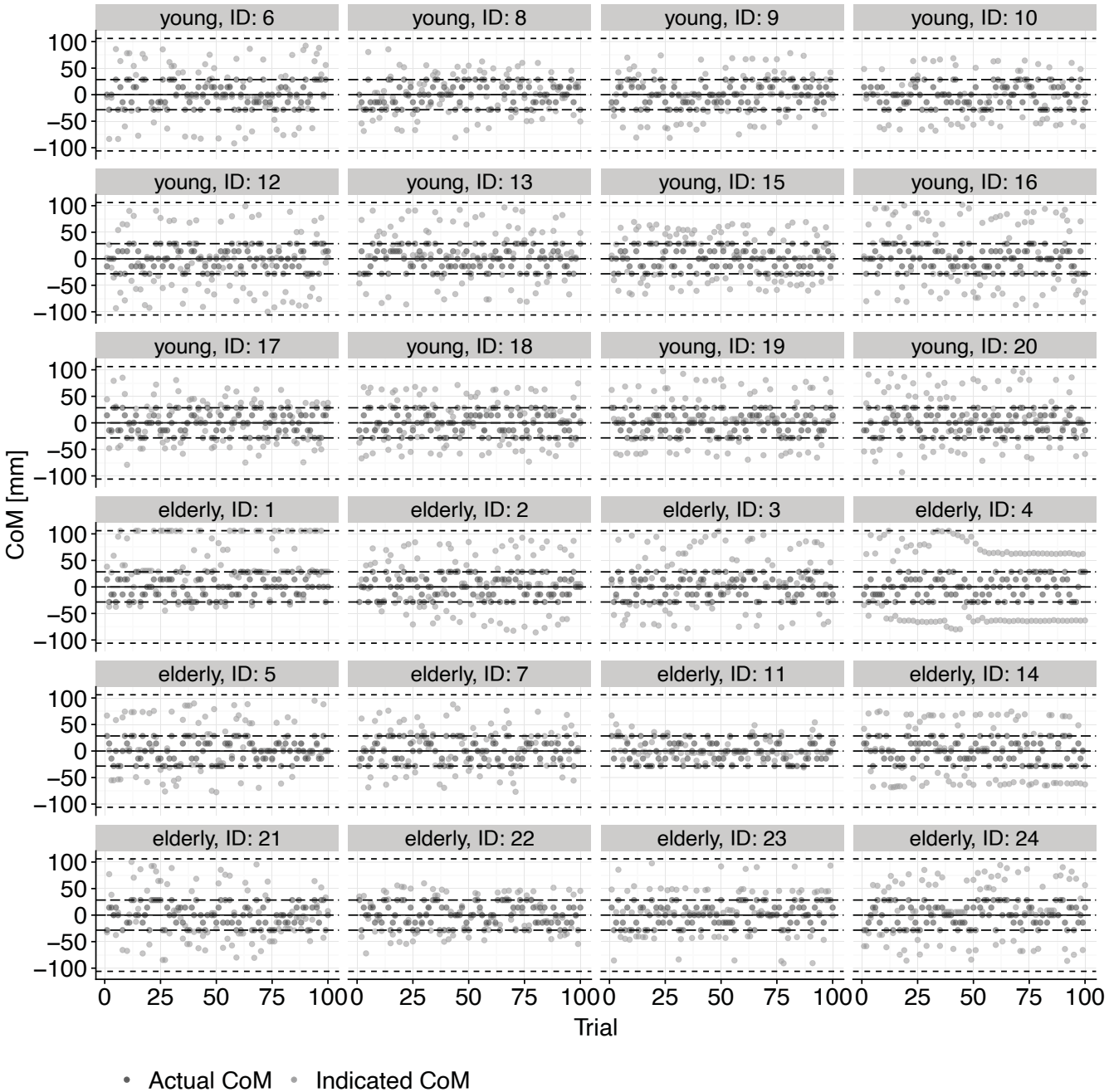

Torque at lift onset [Nm]
0.2
0.1
0.0
−0.1
−0.2
0
25
50
75
100
Trial
age group
young
elderly

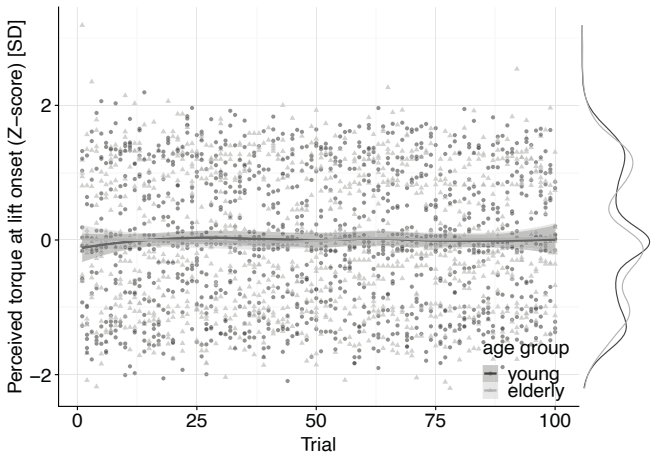

A
young
elderly
Torque at lift onset [Nm]
External torque at the previous trial [Nm]
B
Torque at liftoff [Nm]
Planning error at the previous trial WP [Nm]
C
Torque at liftoff [Nm]
External Torque [Nm]
D
Torque at liftoff WP [Nm]
Perceived torque at the previous trial WP (Z−score) [SD]
E
Torque at lift onset [Nm]
Torque at lift onset at the previous trial [Nm]

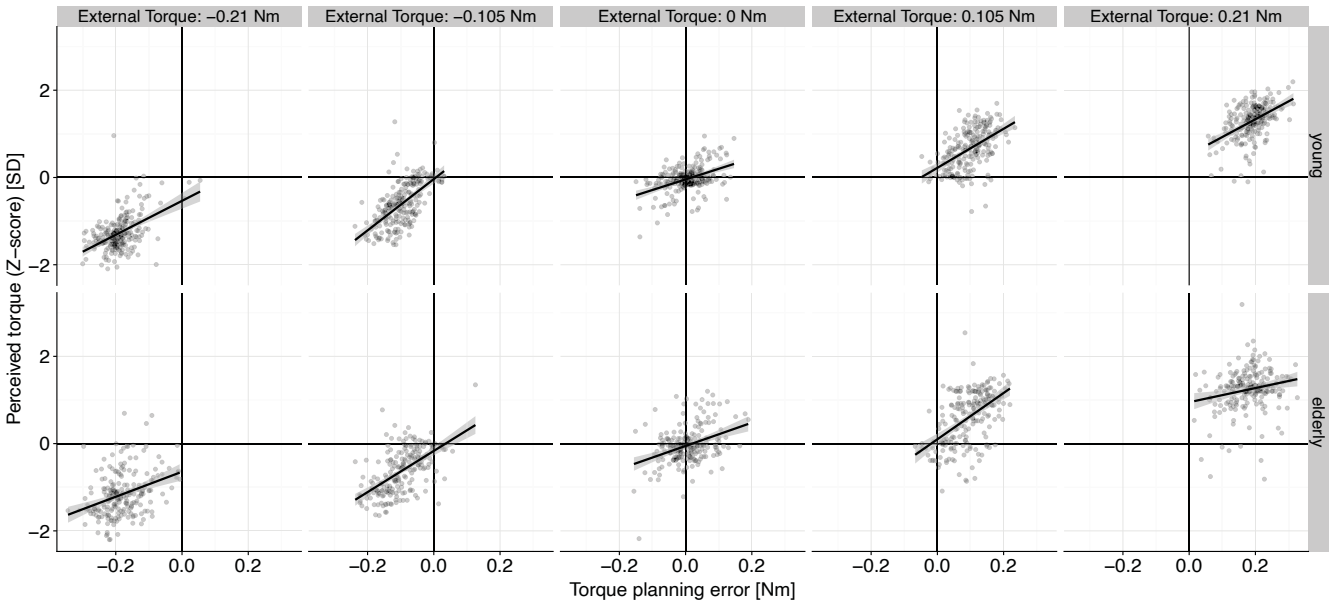

Previous External Torque: −0.21 Nm
Previous External Torque: −0.105 Nm
Previous External Torque: 0 Nm
Previous External Torque: 0.105 Nm
Previous External Torque: 0.21 Nm
young
elderly
Torque at lift onset [Nm]
Torque planning error at the previous trial [Nm]
0.2
0.1
0.0
−0.1
−0.2
−0.2
0.0
0.2

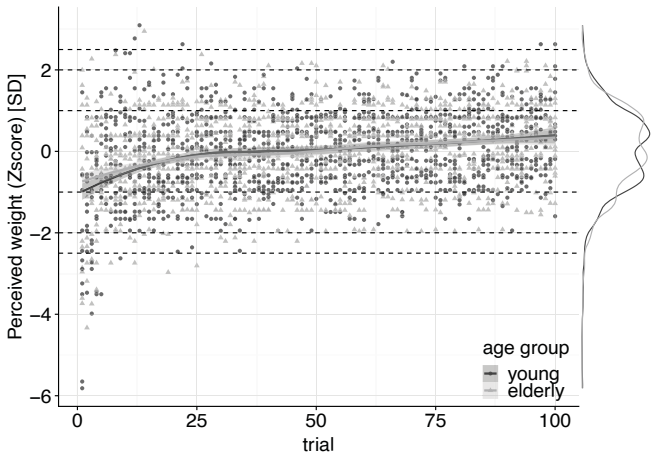

Previous External Torque: −0.21 Nm
Previous External Torque: −0.105 Nm
Previous External Torque: 0 Nm
Previous External Torque: 0.105 Nm
Previous External Torque: 0.21 Nm
young
elderly
Torque at lift onset [Nm]
0.2
0.1
0.0
−0.1
−0.2
−2
0
2
Previously perceived torque (Z−score)[SD]

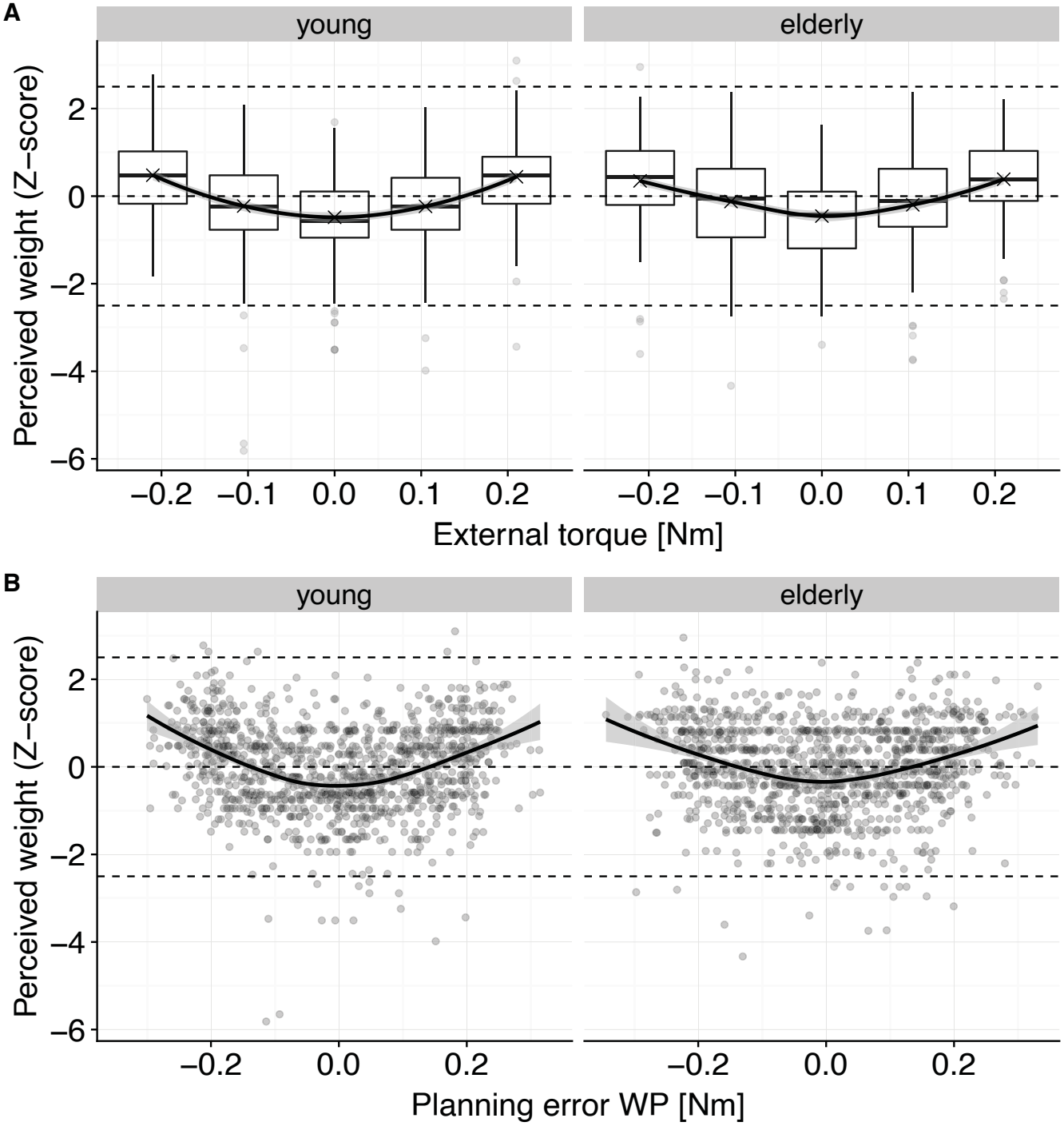

A
young
elderly
Torque at lift onset [Nm]
Previous planning error [Nm]
Previous external torque [Nm]
B
young
elderly
Torque at lift onset [Nm]
Previous planning error [Nm]
Previous Torque at lift onset [Nm]


young, ID: 6
young, ID: 8
young, ID: 9
young, ID: 10
young, ID: 12
young, ID: 13
young, ID: 15
young, ID: 16
young, ID: 17
young, ID: 18
young, ID: 19
young, ID: 20
elderly, ID: 1
elderly, ID: 2
elderly, ID: 3
elderly, ID: 4
elderly, ID: 5
elderly, ID: 7
elderly, ID: 11
elderly, ID: 14
elderly, ID: 21
elderly, ID: 22
elderly, ID: 23
elderly, ID: 24
CoM [mm]
100
50
0
−50
−100
0
25
50
75
100
Trial
Actual CoM
Indicated CoM


Perceived torque at lift onset (Z−score) [SD]
2
0
−2
0
25
50
75
100
Trial
age group
young
elderly


External Torque: −0.21 Nm
External Torque: −0.105 Nm
External Torque: 0 Nm
External Torque: 0.105 Nm
External Torque: 0.21 Nm
young
elderly
Perceived torque (Z−score) [SD]
Torque planning error [Nm]
2
0
−2
−0.2
0.0
0.2


Perceived weight (Zscore) [SD]
2
0
−2
−4
−6
0
25
50
75
100
trial
age group
young
elderly


A
young
elderly
Perceived weight (Z−score)
2
0
−2
−4
−6
−0.2
−0.1
0.0
0.1
0.2
External torque [Nm]
B
young
elderly
Perceived weight (Z−score)
2
0
−2
−4
−6
−0.2
0.0
0.2
Planning error WP [Nm]